Resisting false recognition: An ERP study of lure discrimination.

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Abstract

There is keen interest in what enables rememberers to differentiate true from false memories and which strategies are likely to be the most effective. This study measured electrical brain activity while healthy young adults performed a mnemonic discrimination task, deciding whether color pictures had been studied, were similar to studied pictures (lures), or were new. Between 500 – 800 ms post-stimulus, event-related potentials (ERPs) for correctly recognized studied pictures and falsely recognized lures compared to those for correctly rejected novel items had a left centroparietal scalp distribution typical of the parietal old/new effect associated with recollection. This is in line with previous evidence that similar lures may elicit false or phantom recollection as opposed to just familiarity. There was no evidence of a parietal effect for correctly rejected lures as would be expected if recall-to-reject were used. The ERP old/new effects for lures also varied with individual differences in performance. Parietal effects for falsely recognized lures were larger in better performers, who successfully rejected a greater number of lures as "similar". The better performers also showed more pronounced right frontocentral old/new effects between 800 – 1100 ms for correctly rejected and falsely recognized similar lures. The enhancement of false recollection in better performers implies false recognition of lures occurred only when more specific information was recovered about the study episodic. Together, the findings suggest reliance on recollection to decide that items were studied, supported by post-retrieval processing.

Keywords

Episodic memory; false memory; recognition; recollection; ERPs; retrieval; retrieval monitoring

Abbreviations

EEG, ERP, ANOVA, FA, CR, LDI

1. Introduction

It is well established that memory for events (episodic memory; Tulving 1983) can be misleading as well as accurate, with serious practical consequences (for review see Loftus, 2003; Schacter et al., 1998). It is far less clear whether veridical and false memories are fundamentally different in nature, and how rememberers manage to differentiate between them. Of particular recent interest has been false recollection. Recollection involves the retrieval of specific contextual information from the time an event was originally encoded, and is distinguished in recognition tests from a nonspecific sense of familiarity (Yonelinas, 2002). False recollection is likely to be more convincing and difficult to distinguish from veridical memory than false familiarity. The present study used event-related potentials (ERPs) to replicate earlier findings of false recollection of similar lures, and examine how the critical discrimination from studied items is made.

Although it seems obvious that an event that did not happen cannot be recollected, there is now substantial evidence that recollection of the context associated with an actually experienced event can support a person's experience that a different event was, in fact, encountered. This false recollection may be triggered by a novel recognition probe – a lure – which is related to a studied item. The probability of subjective recollection, assessed using "remember" judgments, does not always distinguish true and false recognition (e.g., Roediger and McDermott, 1995; Thomas and Loftus, 2002). People are also able to make source judgments for lures (Payne et al., 1996) which often reflect the context associated with the corresponding studied items (Hicks and Hancock, 2002; Lyle and Johnson, 2006; Kim and Yassa, 2013; but see McCabe and Geraci, 2009). Moreover, reinstatement of study context of lures' associates increases lure errors (Arndt, 2006; see Arndt, 2012, for review).

Leading theoretical accounts of false memory assume that the specificity of processing at encoding and engagement of control at retrieval both influence the probability of later false recollection (see Gallo, 2010). According to activation-monitoring theory (Roediger and McDermott, 1995; Roediger et al., 2001), if a related lure matches information activated in semantic memory during an episode, false recollection can occur. On fuzzy trace theory (Brainerd and Reyna, 1998), if strong gist traces are encoded, similar lures can elicit "phantom recollection" (Brainerd et al., 2001). Rememberers can also distinguish false or phantom recollection from true recollection by controlled post-retrieval processing. Both these accounts specify use of reality monitoring processes which can distinguish recall elicited by lures and studied items, including diagnostic monitoring for recollection and disqualifying monitoring to reject lures when these cue recall of the studied item and context (recall-to-reject; Johnson et al., 1993; Roediger and McDermott, 1995; Clark and Gronlund, 1996; Brainerd et al., 2002). A third possibility is that automatic hippocampal pattern separation is critical for avoiding false recognition (Schacter et al., 1998; Yassa and Stark, 2011). Pattern separation orthogonalizes new memory traces in relation to those already stored, minimizing overlap (McClelland et al., 1995; Treves and Rolls, 1994). Depending on overlap, similar lures may be recognized, and can trigger recollection as well as familiarity (Norman, 2010; Kim and Yassa, 2013).

1.1. ERP studies of false recollection

A number of prior ERP studies have assessed the degree to which false memories elicit recollection, focusing on differences between the neural correlates of true and false recognition. In recognition tests, ERPs elicited by studied items correctly identified as old (hits) are typically positive-going relative to correctly rejected (CR) new items. Of principal interest here is the parietal old/new effect, a positivity for hits relative to new CR from around 500-800 ms after stimulus presentation which is typically maximal over the left parietal scalp and is thought to index recollection, distinguishing it from familiarity (Rugg et al., 1995; see Friedman and Johnson, 2000; Rugg and Curran, 2007). Familiarity is associated with an earlier, mid-frontal positivity at around 300-500 ms post-stimulus (see Rugg and Curran, 2007). The parietal old/new effect is modulated by the amount of recollected material, and recall of contextual information (Duzel et al., 1997; Rugg et al., 1998; Vilberg et al., 2006). A later-occurring positivity over the right frontal scalp, around 1100-1900 ms post-stimulus, has also been implicated in the application of generic control processes to post-retrieval memory judgments (Friedman and Johnson, 2000; Hayama et al., 2008).

Some studies have found reliable parietal old/new effects only for true recognition, suggesting that lure false alarms were more likely driven by familiarity (Curran, 2000; Geng et al., 2007; see also Chen et al., 2012; Finnigan et al., 2002; Wolk et al., 2006). Dennis et al.'s (2012) recent functional magnetic resonance imaging (fMRI) study also showed hippocampal (as opposed to parahippocampal) and early visual cortical activity both distinguished true from false recollection, in line with the view that contextual reinstatement may accompany only veridical recollective experience (see also Cabeza et al., 2001; Okado & Stark, 2003; Karanian and Slotnick, 2014). However, numerous other ERP studies have found that false as well as true recognition can elicit parietal old/new effects, suggesting occurrence of false recollection when studied items and lures are visually similar pictures sharing basic-level category membership (Curran and Cleary 2003; Goldmann et al., 2003) as well as in adaptations of the DRM paradigm (Boldini et al., 2013; Curran et al., 2001; Nessler et al., 2001; Beato et al., 2012; Wiese and Daum, 2006; see also Cheng and Rugg, 2004). These data are consistent with other fMRI and PET studies which have found indistinguishable neural correlates of true and false recognition (e.g., Kahn et al., 2004; Kim & Cabeza, 2007). Duzel et al. (1997) also showed that equivalent parietal effects for true and false subjective recollection were associated with subjective recollection, defined by "remember" judgments in a DRM variant task (see also Johnson et al., 1997).

Together, the ERP data suggest that lures frequently elicit recollection in these paradigms. However, it is still unclear how people successfully make lure rejection decisions. Goldmann et al. (2003) proposed that post-retrieval control may be critical based on the finding that late, right frontal ERP old/new effects differed between items correctly and falsely judged "old", both of which also elicited parietal effects (see above). However, other studies have not found such a difference (Duzel 1997; Nessler 2001; Boldini et al., 2013; Beato et al., 2012; Wiese and Daum, 2006; see also Cheng and Rugg, 2004). A fuller answer to the question of how people successfully distinguish between studied items and lures requires examination of how correctly rejected lures are processed, and how this processing differs from that of lures incorrectly judged "old".

Curran et al. (2000) reported a parietal ERP effect for correctly rejected plurality-altered word lures (although measured relative to studied item misses rather than rejected new items). As falsely recognized lures did not elicit a parietal effect, the data are most consistent with use of a recall-to-reject monitoring strategy, although the late frontal old/new effect was only reliable for falsely recognized lures suggesting post-retrieval processing may not have contributed to successful recognition judgments. Goldmann et al. (2003) also found a parietal effect for correctly rejected lures, although it was unclear whether this was as large as the effect for hits and lure false alarms (see also Johnson et al., 1997).

A few studies have also examined associations between ERPs and individual differences in performance to try to elucidate the best strategies for avoiding false recognition, but with inconclusive results so far. Data from Curran et al.'s (2001) DRM variant study were suggestive of a false parietal old/new effect only in better performers, while poorer performers were close to chance and showed a parietal effect for hits only. Larger late frontal effects in better performers for hits and falsely recognized lures were consistent with a role of post-retrieval processing in successful lure rejection, although ERPs for rejected lures were not examined. However, Curran and Cleary (2003) found parietal old/new effects for falsely recognized left-right reversed picture lures only in *poorer* performers. Nessler et al. (2001; Experiment 1) found a similar pattern, and a second experiment manipulating encoding strategy suggested that this was because the poorer performers had relied more on gist processing. Curran and Cleary (2003) also examined ERPs for rejected lures: there was a suggestion of larger parietal effects in better performers in line with greater use of recall-to-reject.

1.2. The present study

The present study focused on comparisons of ERPs elicited by lures correctly rejected as "similar" and those falsely identified as old, and on individual differences in these effects. The task is illustrated in Fig. 1: it employed categorically-related picture stimuli, and used the three-way "same/similar/new" response options introduced by Koutstaal et al. (1999) and subsequently employed in fMRI and behavioral investigations of hippocampal pattern separation (Stark et al., 2013; Yassa and Stark, 2011). In order to reject the similar items as unstudied, participants must not only discriminate old from similar items, but positively identify the similar items. This task has been shown to improve lure rejection relative to simple recognition (Koutstaal et al., 1999) and is proposed to place greater demands on neural pattern separation than simple recognition (Stark et al., 2013). The first aim of this experiment was to assess evidence for recollection of correctly rejected as well as falsely recognized lures. The main measure of interest was the parietal old/new effect. In line with previous ERP studies of false recognition, it was expected that this would be observed for false alarms to similar items as well as for hits to old items. Substantial parietal effects for rejected relative to falsely recognized lures would suggest predominant use of the specific retrieval monitoring strategy of recall-to-reject. Conversely, greater parietal effects for falsely recognized than for rejected lures would suggest that lures eliciting recollection are mainly accepted as studied, consistent with false or phantom recollection. Late right frontal effects for accepted and rejected lures as well as hits were also expected if post-retrieval control is important

for lure rejection. The combined pattern of parietal and late anterior old/new effects is therefore informative about the role of recollection and of specific monitoring strategies in lure discrimination.

The second aim was to examine how ERP effects tracked individuals' ability correctly to reject the lures as "similar", to provide information about how this is most effectively achieved. The lure discrimination index (LDI) was defined as the proportion of correctly identified lures corrected for the baseline rate of "similar" responses to novel items. This measure has been associated with the integrity of hippocampal pattern separation (Lacy et al., 2011; Yassa et al., 2011; see Stark et al., 2013) but may also reflect other processes contributing to correct rejection of lures. There were two contrasting predictions. If individual differences in mnemonic discrimination reflect variation in the specificity of encoded information, whether this variation is due to differential initial pattern separation or variation in emphasis on item-specific relative to gist processing, parietal effects for falsely recognized lures will be larger in poorer performers because lures are more likely to trigger recollection (Nessler et al., 2001). However, if variation in lure discrimination ability dominates, the opposite pattern should be observed, whether discrimination of true from false memory relies on automatic pattern separation or on controlled post-retrieval processing. Better discrimination by either mechanism implies that only lures eliciting the most specific recollection will be accepted as studied, so false parietal effects will be more pronounced in better performers. It was also possible that greater use of recall-to-reject by better performers, and therefore larger parietal effects for correctly rejected lures, would be observed (Curran et al., 2000; Curran & Cleary, 2003).

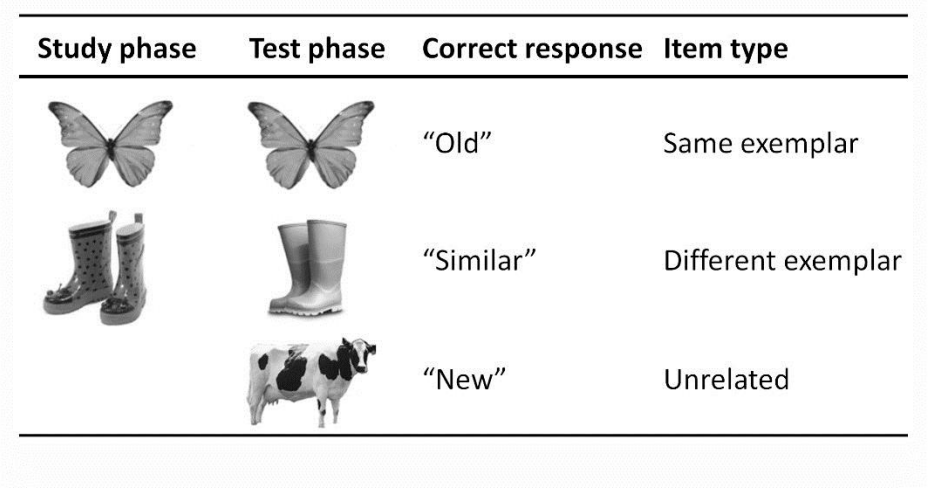

Figure 1. Task and design. Examples of the different stimulus and response conditions are illustrated.

2. Results

Behavioural and ERP data were analyzed for all participants with sufficient artifact-free trials for ERP analysis (N=20, see 4.1). All analyses of variance (ANOVAs) employed a Greenhouse-Geisser correction for nonsphericity by default, and corrected df and p values are reported. The principal experimental conditions of interest for behavioral and ERP analysis were the three correctly identified trial types, and the similar lure

false alarms: Old Hits (studied items attracting correct 'old' responses), Similar FA (similar lures attracting false 'old' responses), Similar CR (similar lures attracting correct 'similar' responses) and New CR (novel items attracting correct 'new' responses).

2.1. Behavioral results

2.1.1. Accuracy

Figure 2 illustrates memory task performance. Analyses of response proportions checked that in the group as a whole, correct responses were more likely than incorrect responses to each item type. Of principal interest was performance for similar lures, and their discrimination from studied and novel items. Participants judged studied items correctly as "old" more often than they judged them "similar" ($t(19) = 11.64$, $p < .001$) and judged lures correctly as "similar" more often than they falsely judged them 'old' ($t(19) = 5.33$, $p < .001$). The Lure Discrimination Index (LDI) was defined as the ability to reject similar lures (p("similar" to lure) - p("similar" to novel item)). LDI was greater than zero in the group as a whole ($t(19) = 5.91$, $p < .001$), and as expected it correlated with the ability to discriminate studied items from lures (p(old hit) - p(lure false alarm); $r = .70$, $p < .001$). A higher LDI was also associated with a more conservative criterion for judging items as 'old' as measured with *Br* ($P_{\text{false alarm}}$ /1-[P_{hit} - $P_{\text{false alarm}}$]; $r = -.58$, $p = .005$) (Snodgrass & Corwin 1988).

2.1.2. Response times

Analysis of median response times (RTs) focused on comparison of the main experimental conditions from which ERPs were formed. ANOVA with the factor of condition (Old Hits, Similar FA, Similar CR and New CR) revealed a main effect ($F(2.0, 38.5) = 17.74$, $p < .001$). *Post hoc* tests (alpha = .01) showed that responses were significantly faster for Old Hits than for Similar FA ($t(19) = 4.12$, $p = .001$) and Similar CR ($t(19) = 6.72$, $p < .001$) and new items ($t(19) = 3.55$, $p = .001$; see Fig. 2). Responses were faster for Similar FA than Similar CR ($t(19) = 4.42$, $p < .001$). RTs were also slightly slower for Similar CR than for New CR, and slightly faster for Similar FA than New CR, but these differences were not reliable ($t(19) = 1.56$, $p > .10$ and $t(19) = 2.48$, $p = .023$). Addition of the lure discrimination index (LDI) as a covariate (see 2.2.1) did not yield any significant results.

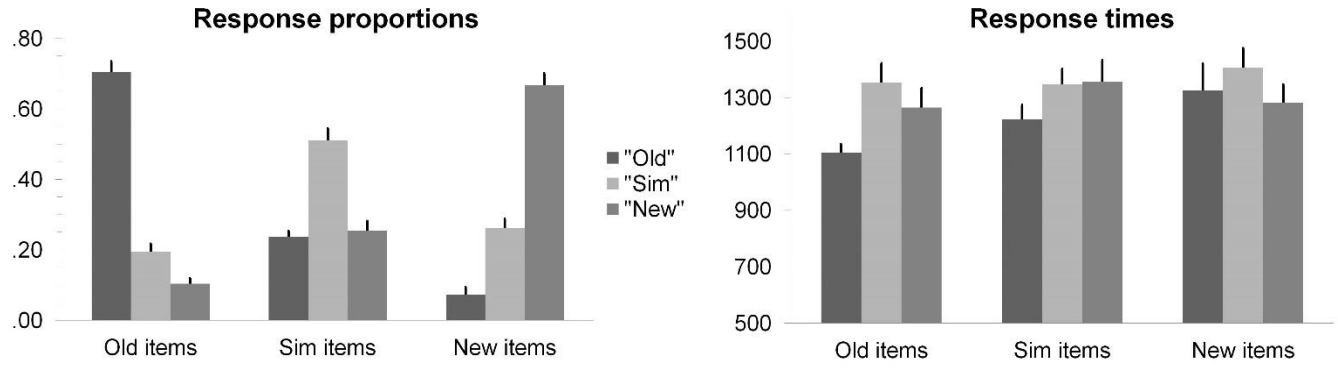

Figure 2. Memory task performance. The plot on the left shows average response proportions, and the plot on the right shows average response times per condition. Old refers to studied items, Sim to unstudied similar lures, and New to novel items (see Fig. 1 and 2.2 for details). Error bars represent the standard error of the mean.

2.2. ERP results

Grand average ERP waveforms elicited by Old Hits, Similar FA, Similar CR and New CR are shown in Fig. 4 for the selected electrode clusters, and mean amplitudes of the principal effects in Fig. 5. The mean numbers of trials (range in brackets) contributing to individual subjects' ERPs in these four conditions were 107 (54 – 142), 33 (14 – 72), 79 (33 – 127) and 100 (46 – 135), respectively. Notably, ERPs to Old Hits were generally more positive-going than ERPs to new CR. From around 300 – 500 ms post-stimulus this positivity had a mid-frontal maximum, and between 500 – 800 ms it had a left centroparietal maximum. During these epochs ERPs to Similar FA and Similar CR were also somewhat more positive-going than those to New CR but if anything less positive than ERPs to Old Hits. Between 800 – 1100 ms a similar pattern of condition differences was maximal over midline central and right frontal sites. From around 1100 ms old/new effects were less pronounced in magnitude, did not differ between conditions and continued to have a right frontocentral maximum. Scalp topography for each time window analyzed is illustrated in Fig. 6, and ERP-performance associations for the middle two epochs are shown in Fig. 7.

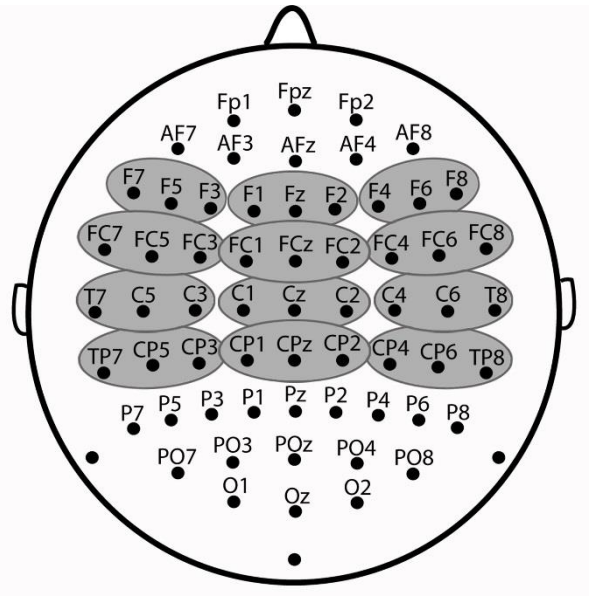

Figure 3. Electrode montage and groupings. The electrode clusters used for analysis are displayed on the international 10-20 head montage used for recording (see 4.5 for details).

2.2.1. Analysis strategy

ERPs were quantified by measuring the mean amplitudes of old/new effects. For convenience, the term "old/new effect" is used to refer to comparisons of Old Hits, Similar FA and Similar CR with New CR. Old/new effect amplitudes were computed as the average ERP for each subject elicited by Old Hits, Similar

FA and Similar CR, after subtraction of the average ERP elicited by New CR. Time windows and electrode sites for amplitude analysis were decided on the basis of prior studies. The principal analysis focused on the parietal old/new effect, from 500 – 800 ms at central and centroparietal groupings (left, midline and right; see 4.4 and Fig. 3 for electrode groupings). The mid-frontal effect was also examined from 300 – 500 ms at frontal groupings (left, midline and right), and late right frontal effect was assessed from 800 – 1100 ms across all electrode groupings.

For each time window, ANOVA with the principal factor of Condition (Old Hits/ Similar FA/ Similar CR) first assessed the amplitude of old/new effects and their modulation by experimental condition, across the electrode sites of interest. Associations between performance for similar items and old/new effect magnitude were then tested using the lure discrimination index (LDI) as a covariate. This indexed correct lure identification, corrected for responses to novel items (see 2.1.1). Because LDI correlated with response criterion as measured with *Br* (see 2.1.1), check analyses were performed in all cases of significant associations between the discrimination covariate and ERPs. These tested whether significant effects were driven by associations between ERP effects and *Br* by a) assessing associations with *Br* as the only covariate, and b) adding *Br* as an additional covariate. In no case did interactions between *Br* and condition approach significance (details are available from the author on request).

Where amplitude analysis suggested that the distribution of old/new effects differed according to condition within a time window, scalp topographies were compared across conditions after rescaling using the range method to remove confounding effects of differences in overall amplitude (McCarthy and Wood, 1985). Topographic analyses were also conducted comparing time windows to assess whether scalp topographies changed over time. All rescaled analyses included data from all 12 electrode groupings (Fig. 3).

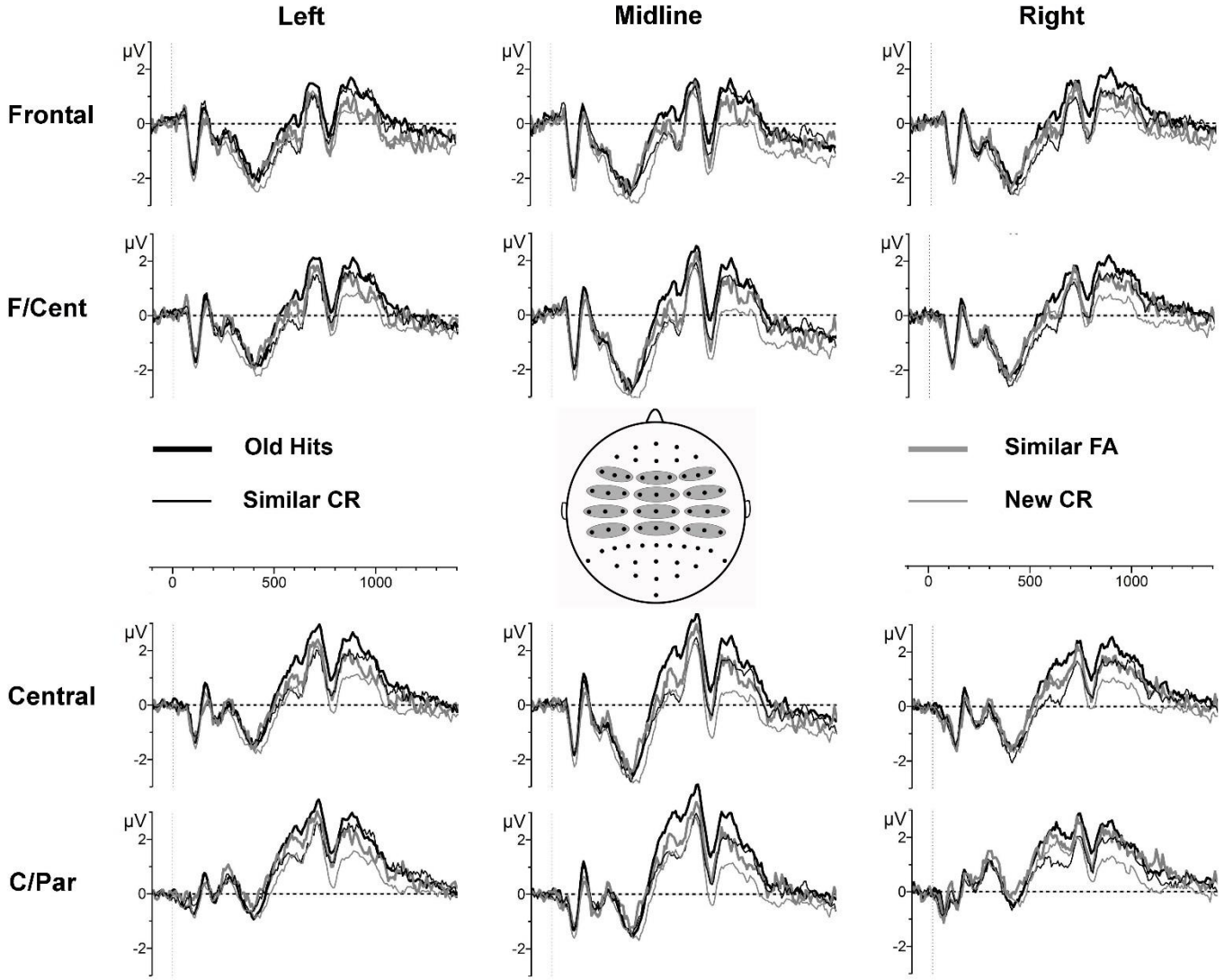

Figure 4. Grand-average ERP waveforms. Waveforms show cross-participant grand-average waveforms for the 12 electrode clusters analyzed. The 4 conditions included are Old Hits (studied items attracting correct 'old' responses), Similar FA (similar lures attracting false 'old' responses), Similar CR (similar lures attracting correct 'similar' responses) and New CR (novel items attracting correct 'new' responses). Positive-going ERPs are plotted upwards. See 2.2.1 for details of ERP analysis strategy.

500 – 800 ms: parietal old/new effects

ANOVA with factors of Condition (Old Hits, Similar FA, Similar CR), Hemisphere (Left, Midline, Right) and anterior-posterior (AP) electrode chain (Frontocentral, Central, Centroparietal) showed a significant main effect of Condition $F(1.8, 35.1) = 4.14$, $p = 0.024$, a main effect of Hemisphere ($F(7.0, 29.0) = 5.95$, $p = 0.007$) and a significant intercept (i.e., overall old/new effect; $F(1, 19) = 5.15$, $p = .035$; for other effects, $p > .1$). Pairwise *post hoc* tests showed that this old/new effect was larger for Old Hits than for Similar CR ($F(1, 19) = 11.60$, $p = .003$). The magnitude of the parietal effect for Similar FA was intermediate between those for Old Hits and Similar CR, but neither difference was significant ($F(1, 19) = 2.07$, $p = .17$, and $F(1,19) = 1.55$, $p = .23$); see Fig. 5. The effect was significant in the group as a whole for Old Hits only ($F(1,19) = 13.02$, $p = .002$; for Similar FA, $F(1,19) = 1.45$, $p = .072$; for Similar CR, $F < 1$).

There were also individual differences in the magnitude of the parietal effect for Similar FA, illustrated in Figure 7. When LDI (see 2.1.1) was added as a covariate, the Condition by LDI interaction was significant ($F(2.0, 36.0) = 7.65$, $p = .002$ (for main effect of Condition, $F(2.0, 36.0) = 7.45$, $p = .002$; for LDI, $F(1, 18) = 9.38$, $p = .007$). Pairwise *post hoc* tests showed that this interaction was driven by the Similar FA condition, which differed from Old Hits ($F(1, 18) = 11.82$, $p = .003$) and from Similar CR ($F(1, 18) = 11.26$, $p = .004$; for Old Hits vs. Similar CR, $F < 1$). Old/new effects at their maximum (at the central midline electrode grouping, i.e., [C1, Cz, C2]) correlated most positively with LDI for Similar FA ($r = .68$; for Similar CR, $r = .43$; for Old Hits, $r = .29$). Thus, parietal old/new effects elicited by similar items falsely recognized as old were larger in better performers.

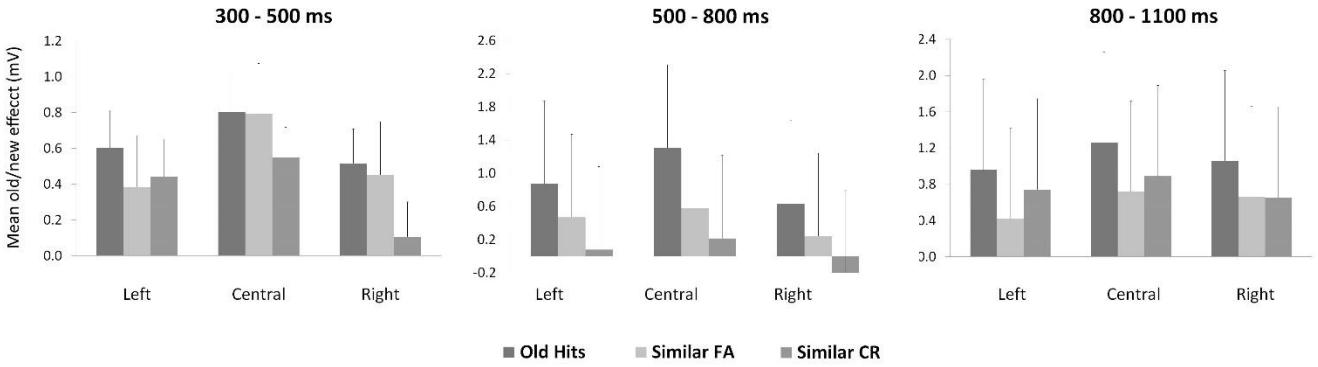

Figure 5. Mean amplitudes (and standard errors) of old/new effects (ERPs to Old Hits, Similar FA and Similar CR each after subtraction of ERPs elicited by New CR) in the time windows 300 – 500 ms, 500 – 800 ms, and 800 – 1100 ms. In the second two epochs, effects are averaged across the AP electrode groupings analyzed (for 500 – 800 ms, these were Frontocentral, Central and Centroparietal groupings and for 800 – 1100 ms, all four groupings; see Fig. 3, and 2.2.1 for analysis strategy).

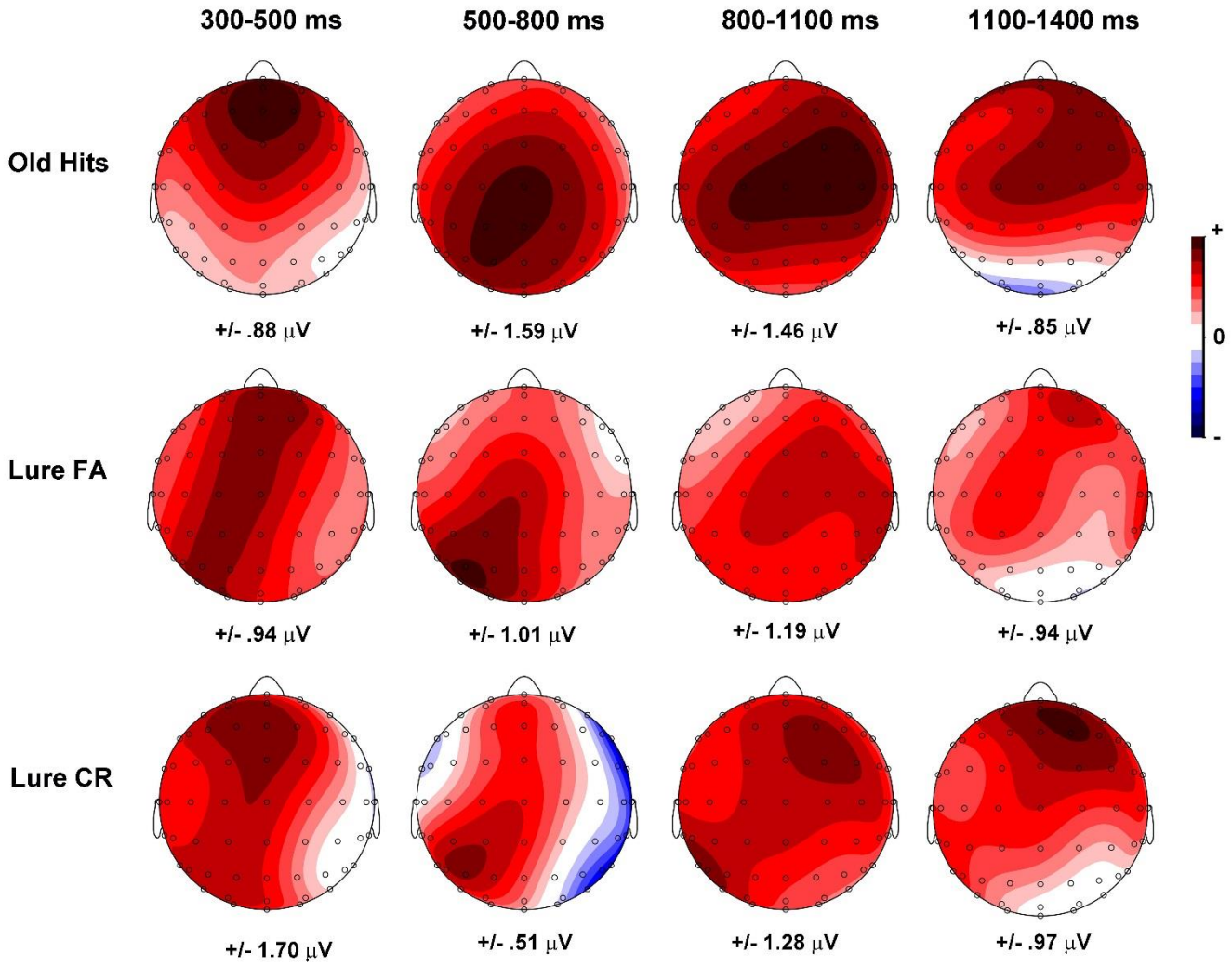

Figure 6. Scalp distribution of ERP old/new effects. Scalp topographies are shown of the between-condition differences in mean ERP amplitude in the four time windows analyzed. The plots are of the old-new or similar-new subtractions for Old Hits, Similar FA, and Similar CR (see Fig. 5 and 2.2.1 for details). Maps are scaled to the maxima (red) of each effect, and the ranges are displayed under each map in microvolts.

2.2.2. 300 – 500 ms: mid-frontal old/new effects

ANOVA with factors of Condition and Hemisphere (Left, Midline, Right) on old/new effects from the frontal electrode groupings showed a reliable overall effect (for intercept, $F(1, 19) = 9.42$, $p = .006$) and a main effect of Hemisphere ($F(1.8, 33.8) = 5.09$, $p = .014$), reflecting the expected midline maximum of the old/new effect (see Figs 5 and 6). When LDI was added as a covariate, there was a reliable main effect of Condition ($F(1.9, 33.9) = 4.51$, $p = .020$) and interaction of Condition with LDI ($F(1.9, 33.9) = 4.81$, $p = .016$). *Post hoc* tests showed that this interaction was mainly driven by differences between Old Hits and Similar FA (for pairwise Condition x LDI, $F(1, 18) = 11.83$, $p = .003$; for Old Hits vs. Similar CR, $F(1, 18) = 4.47$, $p = .049$; for Similar FA vs. Similar CR, $F < 1$). For Old Hits, the old/new effect tended to correlate negatively with LDI ($r = -.31$, $p = .075$), whilst for Similar FA the association was non-significant but numerically positive ($r = .32$, $p = .22$; for Similar CR, $r = .01$, $F < 1$). At the mid-frontal cluster at which the mid-frontal old/new effect is typically

maximal, the effect was also reliable in the group as a whole for Old Hits and Similar FA ($t(19) = 2.80$, p = .011; $t(19) = 2.95$, p = .008) but not for Similar CR ($t(19) = 1.86$, p = .079; alpha = .017). Thus, participants with better lure rejection performance tended to show smaller mid-frontal effects than poorer performers for Old Hits only.

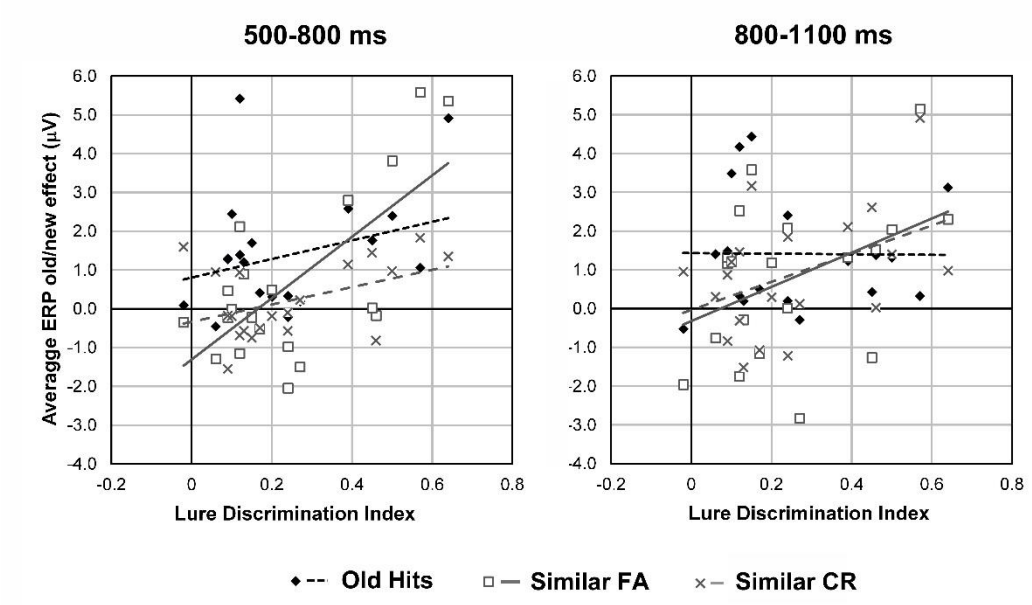

Figure 7. Old/new effects and lure discrimination performance. Scatter plots show ERP old/new effects in the 500-800 and 800-1100 ms epochs at the same Central electrode grouping (average of [C1, Cz, C2]; see 2.4), illustrating their different associations with performance indexed by LDI (see 2.2.1 and Fig. 5 for definition of old/new effects, and 2.1.1 for definition of LDI).

2.2.3. 800 – 1100 ms: late old/new effects

ANOVA with factors of Condition, Hemisphere (Left, Midline, Right) and anterior-posterior (AP) electrode chain (Frontal, Frontocentral, Central, Centroparietal) showed a reliable average old/new effect across conditions (for intercept, $F(1,19) = 12.13$, p = .002) and a marginal effect of Hemisphere reflecting a tendency to a midline to right sided maximum ($F(1.9, 35.3) = 3.66$, p = .070), but no effects of Condition (max $F = 1.74$, p > .10); see Figs. 5 and 6. *Post hoc* tests indicated significant old/new effects in the group as a whole for Old Hits and – unlike in the earlier epochs – for Similar CR (for intercept, $F(1,19) = 16.11$, p = .001; $F(1,19) = 9.11$, p = .007; for Similar FA, $F(1,19) = 2.95$, p > .10).

Addition of LDI as a covariate revealed a significant main effect of Condition ($F(1.8, 32.7) = 5.36$, p = .012) and a Condition by LDI interaction ($F(1.8, 32.7) = 3.86$, p = .035). *Post hoc* tests showed that – unlike in the earlier epochs – this was driven by both similar lure conditions, although effects for Old Hits were slightly larger in the group as a whole (see Fig. 7; for the pairwise comparison of Condition x LDI for Old Hits vs. Similar FA, $F(1,18) = 10.29$, p = .005; for Old Hits vs. Similar CR, $F(1,18) = 3.74$, p = .069; for Similar FA vs. Similar CR, $F < 1$). For both Similar FA and Similar CR, old/new effects were positively correlated with LDI at their maximum at the central midline electrode grouping ([C1, Cz, C2]; r = .41; r = .43), unlike for Old

Hits (r = -0.01). Thus, in this time window old/new effects were larger for both Similar FA and Similar CR in participants who were better able to correctly identify the similar items (see Fig. 7).

2.2.5 Topographic analyses comparing time windows

Analysis of rescaled data demonstrated the expected differences in scalp topography between the mid-frontal and parietal old/new effects: ANOVA with the additional factor of time Window (300-500 ms, 500-800 ms) showed a significant interaction of Window with AP chain across conditions ($F(1.3, 25.5) = 5.73$, $p = .017$), reflecting the earlier frontal and later centroparietal and parietal maxima of these effects. No effects involving the factor of Condition were reliable.

Comparison between the 500 – 800 ms and 800 – 1100 ms time windows showed a change in the scalp topography of old/new effects between the two which approached significance when all conditions were analyzed together (for Window x Hemisphere, $F(1.9, 36.9) = 2.94$, $p = .067$; for Window x Hemisphere x Condition, $F < 1$). However, when the largest old/new effects, those for Old Hits, were considered alone, their lateralization differed significantly between the two time windows (for Window x Hemisphere, $F(1.6, 30.5) = 3.68$, $p = .046$). The predominantly midline scalp distribution shifted from midline-left to a more right-sided distribution (see Figs. 5 and 6).

3 Discussion

This experiment used ERPs to investigate the processes by which people avoid false recognition and correctly reject items similar to, but not the same as, those they have previously encountered. Using a recognition task which required explicit identification of similar lures as well as studied items, we replicated previous findings of parietal old/new effects for falsely recognized lures, suggestive of false recollection. In the group as a whole these effects were somewhat attenuated relative to those elicited by correctly recognized studied items. However, parietal and right frontal ERP old/new effects also varied in magnitude according to individual ability correctly to reject lures as "similar". The data, discussed in detail below, conform to the pattern predicted if recollection predominantly supports false recognition, not rejection, of lures, but lure recollection is less likely, and perhaps less specific, in better performers. They also implicate post-retrieval monitoring processes in lure discrimination.

3.2 Behavioral findings

Participants were able to discriminate studied from similar items effectively, and their ability to do this correlated with their ability correctly to reject the similar lures. Hit responses were the fastest, suggesting that many studied items were quickly recognized compared to lures and new items. False alarms to similar items were also faster than correct rejections of these items, consistent with engagement of additional processes during successful lure rejection relative to false recognition, although there was no ERP evidence for use of a recall-to-reject strategy (see below). There were no reliable associations between response times and

individual differences in lure rejection ability, so the findings of such associations for the ERP data are not confounded by differential time on task.

3.3 ERP findings

Analysis of the ERP data showed a typical pattern of more positive-going activity for correctly recognized studied items (hits) than for correctly rejected new items in the three time windows analyzed. The ERPs elicited by falsely recognized and correctly rejected similar lures showed lesser degrees of positivity which varied according to the epoch and individual differences in performance.

3.3.1 Parietal old/new effect

Of principal interest was the parietal old/new effect between 500-800 ms, indexing recollection (see Introduction, and Rugg and Curran, 2007, for review). As expected, ERPs for hits showed a prominent positivity in this epoch with a left centroparietal maximum. A smaller parietal effect was also present for falsely recognized lures, which was also larger in better than in poorer performers, an association which differed significantly both from hits and lure CR. There was no evidence of a parietal effect for correctly rejected lures. Together with the late anterior effects, discussed below, this suggests that although retrieval monitoring played a role, use of recall-to-reject strategies was not prominent (see 3.4). Instead, the data suggest that falsely recognized lures were more likely to be recollected in the better performers, or that more information was recollected (Vilberg & Rugg, 2006). Recollection as indexed by the parietal effect also distinguished falsely recognized lures from correctly rejected lures in proportion to individual ability to identify the lures behaviorally.

These findings are consistent with the earlier study of Curran et al. (2001) in which only better performers appeared to show false recollection. However, they differ from those of two other studies which found evidence of false recollection only in poorer performers (Curran and Cleary, 2003; Nessler et al., 2001). This is unlikely to be due to task differences: Curran and Cleary's (2003) study was most similar to the present study in using pictorial stimuli, whereas Curran et al. (2001) and Nessler et al. (2001) used verbal stimuli. Gross level of performance also cannot explain the different findings. Although raw false recognition rates were comparable in the sub-groups showing false recollection in Curran et al.'s (2001) and Curran and Cleary's (2003) studies (.49 and .50), they were also closer to the rates in Nessler et al.'s (2001) better performers who did *not* show evidence of false recollection (.39 versus .15). However, it is difficult to make close comparisons with the present study because in these prior studies, raw lure false alarm rates rather than corrected lure rejection rates were used to define level of performance. It is likely that different factors accounted for the two previous findings of parietal effects for falsely recognized lures only in poorer performers, and that neither of these factors dominated in the current study. Nessler et al. (2001) attributed their result to variation in lure activation reflecting different degrees of reliance on gist processing at encoding. This variation was found only in the experiment which used an intentional study task, unlike in the current study. As noted in the Introduction (1.2), the direction of our individual differences association is also

incompatible with dominance of different degrees of gist processing or specificity of encoding in determining better performance. In Curran and Cleary's (2003) study, lure parietal effects followed a different pattern from the present study, as better and poorer performers did not differ only in the parietal effect elicited by falsely recognized lures. There was also evidence that the higher performers used recall-to-reject: their parietal old/new effect for rejected lures was almost identical in magnitude to the effect for hits, unlike in the present study. Thus although in both Curran and Cleary's (2003) study and the present study the better performers showed evidence of more effective monitoring (discussed further below, see 3.3.3 and 3.4), the current data support use of diagnostic as opposed to disqualifying strategies.

3.3.2 Mid-frontal old/new effect

A mid-frontal old/new effect between 300 – 500 ms post-stimulus also distinguished the conditions and differed according to level of performance. It was topographically as well as temporally distinct from the parietal effect, consistent with previous studies and different underlying neural generators (Rugg & Curran, 2007). The mid-frontal effect was more pronounced for recognized old items and falsely recognized lures than for correctly rejected lures. Assuming that the mid-frontal old/new effect reflects familiarity as opposed to recollection (for discussion see Bridger et al., 2012; Voss and Federmeier, 2011), this suggests that some lures were recognized on this basis. Poorer performers also showed larger mid-frontal effects for old hits than better performers. This raises the possibility that poorer performers relied more on familiarity for making their judgments about old items. This would be consistent with the assumption that reliance on familiarity is an ineffective strategy for avoiding false recognition, because it is elicited by lures as well as by studied items, sometimes strongly (for reviews see Schacter and Slotnick, 2004; Yonelinas, 2002). However, the present data do not clearly support use of such a strategy in the poorer performers, since it predicts they will also show the largest mid-frontal effects for falsely recognized lures, and this behavioral association was non-significant. Instead, it appears that false (as well as true) recognition was associated with familiarity in the group as a whole. Most importantly, early mid-frontal responses did not distinguish reliably between lures which were falsely recognized and those which were correctly rejected, suggesting that some subsequent processing of lures was critical for this decision.

3.3.3 Late old/new effects

Both similar lures and studied items also elicited a late old/new effect between 800 and 1100 ms post-stimulus with a right frontocentral maximum, which was topographically distinct from the parietal old/new effect. As for the parietal effects, in the group as a whole this effect was most prominent for hits, but its modulation by individual differences in performance differed from the previous epoch: the late old/new effect was significantly more prominent in better performers for lure CR as well as for lure FA.

The timing and distribution of this late old/new effect is consistent with previous findings of post-retrieval activity maximal over right frontal scalp (see Introduction). Right frontal old/new effects are thought to reflect generic control processes involved in task-relevant decisions including those regarding what is remembered

(Friedman and Johnson, 2000; Hayama et al., 2008). These effects onset from as early as 800 ms post-stimulus, directly following offset of the parietal effect and persisting as late as 1900 ms post-stimulus (e.g., Cruse and Wilding, 2011; Senkfor and Van Petten, 1998; Wilding and Rugg, 1996; Woodruff et al., 2006). In the present study, right frontal effects were also observed up to 1400 ms post-stimulus (not reported), but only varied according to condition and performance from 800 – 1100 ms. Given that average RTs to Old Hits, Similar FA and Similar CR were 1105, 1222 and 1348 ms, these performance associations presumably occurred after recollection but prior to responding. It is therefore likely that the processes reflected in the late old/new effect contributed to decision processes. This suggests that after initial recognition, further processing occurred in all participants prior to making the "old" decision, but engagement of these post-retrieval processes for lure items was greatest in the better performers.

3.4 General Discussion

The present data provide new information about how people discriminate novel items from similar items they have previously encountered in order to avoid false recognition. In line with earlier studies, a parietal effect was elicited by recognized items, whether studied or lures. However, unlike in some earlier studies, it was not significant for lures which were correctly rejected. This suggests that decisions that items were "old" were associated with recollection, whilst lures were correctly judged "similar" in its absence. Therefore, the explicit emphasis on lure identification in this task (Koutstaal et al., 1999; Stark et al., 2013) did not necessitate use of a recall-to-reject strategy, although such a strategy can be successful in similar tasks (Curran, 2000; Curran and Cleary, 2003; Kim and Yassa, 2013). Together, the data suggest that performance was supported by diagnostic post-retrieval processing to detect recollection.

As noted in the Introduction, the parietal effect has been shown to be larger in magnitude when more information is recollected, and is associated with source recall (Rugg et al., 1998; Wilding, 2000; Vilberg et al., 2006; for reviews see Friedman & Johnson, 2000; Rugg and Curran, 2007). As outlined in the Introduction, lure false recollection is accommodated by all three theoretical accounts. The positive association between the parietal effect magnitude for false alarms and lure discrimination performance further suggests that although fewer lures were falsely recognized, these were more likely to be associated with recollection in better performers, or more specific information was recalled. This implies variation in the effectiveness of retrieval processing, either automatic pattern separation of lures, post-retrieval processing, or both. The existence of individual differences in hippocampal pattern separation and completion is consistent with fMRI evidence in healthy young (Chadwick, Bonnici, & Maguire, 2014) and older adults (e.g., Stark, Yassa, & Stark, 2010). However, a post-retrieval processing interpretation is supported by the finding that right frontal effects for both falsely recognized and correctly rejected lures also distinguished better from poorer performers. The timing of the late frontal effect, i.e., after the parietal effect but prior to responding, is in line with this interpretation. One possibility is that participants monitored the *contents* of recollection and rejected items for which the required specific information was not recovered, and that more effective monitoring by better performers meant that only those lures eliciting highly specific recollection were falsely judged "old". This is

consistent with prior behavioral and ERP studies implicating controlled post-retrieval memory monitoring and editing in the avoidance of false recognition (see Friedman and Johnson, 2000; Johnson et al., 1993). Therefore, the most parsimonious account of the present data is consistent with both activation-monitoring and fuzzy trace views, since these specify the importance of post-retrieval monitoring processes for lure discrimination (Roediger and McDermott, 1995; Brainerd et al., 2002). The presence of parietal effects for recognized but not for rejected lures, and the individual differences in parietal effects for recognized lures, also suggests that the monitoring was diagnostic, emphasizing detection of recollection, rather than recall-to-reject. Not enough is known about the factors which support use of specific memory monitoring strategies (see Odegard et al., 2008; Schmid et al., 2010), but behavioral and fMRI data support the notion that these two types of monitoring are dissociable (e.g., Gallo et al. 2006; Gallo et al., 2010).

Although the present data cannot be explained by individual differences in the specificity of encoded memory traces, reflecting variation in either pattern separation or relational or gist processing at encoding, such differences may be emphasized under other conditions. In such cases, parietal old/new effects reflecting gist recollection would be likely present for lure correct rejections as well as false recognition. An example may have been the study of Goldmann et al. (2003), which used a variant on the DRM task (see Introduction). Future studies can examine this possibility by encouraging gist processing through manipulation of study instructions (Nessler et al., 2001) or including either more closely similar lures, or multiple similar items in studied lists (see Koutstaal and Schacter, 1997; Pidgeon and Morcom, 2014). The latter manipulation has the additional benefit of reducing the potential utility of a recall-to-reject strategy (Gallo, 2004), so that evidence for recollection of correctly rejected lures, if present, can be more clearly attributed to recollection of gist. fMRI studies will also be essential for testing the contribution of pattern separation and completion to lure discrimination at encoding and retrieval (Kirwan & Stark, 2007).

The present interpretation of parietal effects rests on some assumptions. The "reverse inference" (see Poldrack, 2006) that these indicate the presence of recollection is based on substantial evidence that in recognition memory studies, parietal old/new effects occur when judgments are based on recollection rather than familiarity (see Friedman & Johnson, 2000; Rugg & Curran, 2007). It is not necessary to assume that this ERP modulation is elicited only by recollection: reverse inference can be used to infer presence of recollection *rather than* familiarity (a model comparison; Machery, 2013; see also Klein, 2012). Less is currently known about the relation between the parietal old/new effect and what is recollected. It has been shown to be larger when more information about the study episode is recollected, operationalized as identifying an associate item and/or incidental, spatial and temporal features of the study context (Vilberg & Rugg, 2006; Vilberg & Rugg, 2009). In future investigations, measurements of the level of specificity of information recovered, and its nature, would enable more direct tests of hypotheses about gist and specific memory, as well as assisting interpretation of differences at the neural level between veridical recollection and false or phantom recollection.

3.5 Conclusions

The present data support the notion that post-retrieval processing is critical for rememberers to avoid falsely recognizing items similar to those previously encountered. The finding of parietal ERP old/new effects for falsely recognized similar lures and for studied items, but not correctly rejected lures, suggests that participants decided which items were studied and which were similar by the presence of significant recollection. Familiarity may have contributed to poorer performers' judgements, although the data were ambiguous in this regard. The observation of late old/new effects which were more marked in better performers for similar items also implicates post-retrieval monitoring in successful lure discrimination. The relative prominence of false recollection effects in better performers further suggests that these participants only classify items as "old" when substantial evidence of recollection is present, perhaps indicating the recovery of more specific content. Together, the findings support existing evidence that false recollection is a relatively common and robust phenomenon, and constrain theoretical accounts of the strategies which can be used to support accurate recognition.

4 Experimental Procedures

4.1 Participants

Twenty-nine healthy young adults aged between 19 and 34 years took part in the study. Of these, 20 (mean age 24.6 years, SD = 3.5 years; 8 male) had sufficient artifact-free trials (>=14) for ERP analysis.

4.2 Stimuli

Stimuli were 480 pairs of images of common objects or animals (photographs or colored drawings, approx. 300 x 270 pixels). Each pair comprised two perceptually similar exemplars of the same basic-level concept, e.g., *window*. Three hundred and five were from Koutstaal's (2006) stimulus set; the remaining were copyright-free images obtained online. During the study phase, 320 critical images were presented. At test, participants viewed 480 critical images, comprising 160 studied images (repetitions of studied items) and 160 similar lures of studied images (the similar items paired with the remainder of the studied items), with 160 novel images. Six counterbalanced stimulus sets rotated stimuli through conditions (studied, lure, novel) and counterbalanced the images within each pair which were presented at study. For study and test phases, a unique random trial order of presentation was generated for each participant. Two stimuli also served as initial filler items at the start of study and test lists. Fifty additional images (including 20 pairs) were used for pre-experimental practice.

4.3 Procedure.

Participants studied pictures of objects, and were later given a recognition test, during which electroencephalogram (EEG) recordings were acquired. In the test phase, they were asked to recognize original studied exemplars of a concept (e.g. a butterfly) as "'old", whilst explicitly rejecting different exemplars of

the same concept as “similar”, and classifying items of a concept not previously presented in the experiment as “new” (Fig. 1).

4.4 EEG recording and analysis

The EEG recordings were acquired at a sampling rate of 1024 Hz using a BioSemi ActiveTwo system (http://www.biosemi.com), and 64 electrodes in an international 10–20 configuration (Fig. 3), as well as two mastoid electrodes and four electrooculogram (EOG) electrodes (at the left and right horizontal canthi, and above and below the right eye). Recordings were referenced to the common mode sense (CMS; active electrode) and grounded to a passive electrode. In pre-processing, the EEG was re-referenced offline to the average of the left and right mastoid, filtered (0.03–70 Hz band-pass filter, plus 50 Hz Notch filter where required), downsampled to 128 Hz, and corrected for artefacts using independent components analysis as implemented in BrainVision Analyzer (Brain Products ©). The data were then divided into epochs with a 100 ms baseline before stimulus onset that lasted until 1500 ms post-stimulus. All epochs were baseline-corrected before being combined to compute condition-averages per participant.

ERP analyses were conducted on pooled data from 12 clusters of electrodes over the frontal (left: [F3, F5, F7], midline: [F1, F2, Fz], right: [F4, F6, F8]), frontocentral (left: [FC3, FC5, FT7], midline: [FC1, FC2, FCz], right: [FC4, FC6, FT8]), central (left: [C3, C5, T7], midline: [C1, Cz, C2], right: [C2, C4, T8]) and centroparietal (left: [CP3, CP5, TP7], midline: [CP1, CPz, CP2], right: [CP2, CP4, TP8]) scalp (see Fig. 3).

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References

Arndt, J., 2006. Distinctive information and false recognition: The contribution of encoding and retrieval factors. Journal of Memory and Language. 54**,** 113-130.

Arndt, J., 2012. False recollection: empirical findings and their theoretical implications. Psychology of Learning and Motivation, Vol 56. 56**,** 81-124.

Beato, S.M., Boldini, A., Cadavid, S., 2012. False memory and level of processing effect: an event-related potential study. Neuroreport. 23**,** 804-808.

Boldini, A., Beato, M., Cadavid, S., 2013. Modality-match effect in false recognition: an event-related potential study. Neuroreport. 24**,** 108-113.

Brainerd, C.J., Reyna, V.F., 1998. When things that were never experienced are easier to "remember" than things that were. Psychological Science. 9**,** 484-489.

Brainerd, C.J., Wright, R., Reyna, V.F., Mojardin, A.H., 2001. Conjoint recognition and phantom recollection. Journal of Experimental Psychology-Learning Memory and Cognition. 27**,** 307-327.

Brainerd, C.J., Wright, R., Reyna, V.F., Payne, D.G., 2002. Dual-retrieval processes in free and associative recall. Journal of Memory and Language. 46, 120-152.

Bridger, E.K., Bader, R., Kriukova, O., Unger, K., Mecklinger, A., 2012. The FN400 is functionally distinct from the N400. Neuroimage. 63**,** 1334-1342.

Cabeza, R., Rao, S.M., Wagner, A.D., Mayer, A.R., Schacter, D.L., 2001. Can medial temporal lobe regions distinguish true from false? An event-related functional MRI study of veridical and illusory recognition memory. Proceedings of the National Academy of Science U S A. 98, 4805-10.

Chadwick, M. J., Bonnici, H. M., & Maguire, E. A. (2014). CA3 size predicts the precision of memory recall. Proceedings of the National Academy of Science U S A, 111(29), 10720-10725.

Chen, H., Voss, J.L., Guo, C., 2012. Event-related brain potentials that distinguish false memory for events that occurred only seconds in the past. Behavioral and Brain Functions. 8, 8-36.

Cheng, S.K., Rugg, M.D., 2004. An event-related potential study of two kinds of source judgment errors. Cognitive Brain Research. 22**,** 113-127.

Clark, S. E., Gronlund, S. D. 1996. Global matching models of memory: How the models match the data. Psychonomic Bulletin & Review. 3, 37–60.

Cruse, D., Wilding, E.L., 2011. Temporally and functionally dissociable retrieval processing operations revealed by event-related potentials. Neuropsychologia. 49**,** 1751-1760.

Curran, T., 2000. Brain potentials of recollection and familiarity. Memory & Cognition. 28**,** 923-938.

Curran, T., Schacter, D.L., Johnson, M.K., Spinks, R., 2001. Brain potentials reflect behavioral differences in true and false recognition. Journal of Cognitive Neuroscience. 13**,** 201-216.

Curran, T., Cleary, A.M., 2003. Using ERPs to dissociate recollection from familiarity in picture recognition. Cognitive Brain Research. 15**,** 191-205.

Deese, J., 1959. On the prediction of occurrence of particular verbal intrusions in immediate recall. Journal of Experimental Psychology. 58**,** 17-22.

Dennis, N.A., Bowman, C.R., Vandekar, S.N., 2012. True and phantom recollection: An fMRI investigation of similar and distinct neural correlates and connectivity. Neuroimage. 59**,** 2982-2993.

Duzel, E., Yonelinas, A.P., Mangun, G.R., Heinze, H.J., Tulving, E., 1997. Event-related brain potential correlates of two states of conscious awareness in memory. Proceedings of the National Academy of Sciences U S A. 94**,** 5973-5978.

Finnigan, S., Humphreys, M.S., Dennis, S., Geffen, G., 2002. ERP 'old/new' effects: memory strength and decisional factor(s). Neuropsychologia. 40**,** 2288-2304.

Fraser, C.S., Bridson, N.C., Wilding, E.L., 2007. Controlled retrieval processing in recognition memory exclusion tasks. Brain Research. 1150**,** 131-142.

Friedman, D., Johnson, R., 2000. Event-related potential (ERP) studies of memory encoding and retrieval: A selective review. Microscopy Research and Technique. 51**,** 6-28.

Gallo, D.A., 2004. Using recall to reduce false recognition: diagnostic and disqualifying monitoring. Journal of Experimental Psychology: Learning, Memory and Cognition. 30**,** 120-8.

Gallo, D.A. Bell, D.M., Beier, J.S., Schacter, D.L. 2006. Two types of recollection-based monitoring in younger and older adults: Recall-to-reject and the distinctiveness heuristic. Memory. 14, 730-41.6.

Gallo, D.A. 2010. False memories and fantastic beliefs: 15 years of the DRM illusion. Memory & Cognition, 38(7), 833-848.

Geng, H., Qi, Y., Li, Y., Fan, S., Wu, Y., Zhu, Y., 2007. Neurophysiological correlates of memory illusion in both encoding and retrieval phases. Brain Research. 1136**,** 154-168.

Goldmann, R.E., Sullivan, A.L., Droller, D.B., Rugg, M.D., Curran, T., Holcomb, P.J., Schacter, D.L., Daffner, K.R., Budson, A.E., 2003. Late frontal brain potentials distinguish true and false recognition. Neuroreport. 14**,** 1717-20.

Hayama, H.R., Johnson, J.D., Rugg, M.D., 2008. The relationship between the right frontal old/new ERP effect and post-retrieval monitoring: specific or non-specific? Neuropsychologia. 46**,** 1211-23.

Hicks, J.L., Hancock, T.W., 2002. Backward associative strength determines source attributions given to false memories. Psychonomic Bulletin & Review. 9**,** 807-815.

Hunsaker, M.R., Kesner, R.P., 2012. The operation of pattern separation and pattern completion processes associated. Neuroscience and Biobehavioral Reviews.

Johnson, M.K., Hashtroudi, S., Lindsay, D.S., 1993. Source monitoring. Psychological Review. 114**,** 3-28.

Johnson, M.K., Nolde, S.F., Mather, M., Kounios, J., Schacter, D.L., Curran, T., 1997. The similarity of brain activity associated with true and false recognition memory depends on test format. Psychological Science. 8**,** 250-257.

Kahn, I., Davachi, L., Wagner, A.D., 2004. Functional-neuroanatomic correlates of recollection: implications for models of recognition memory. Journal of Neuroscience. 24, 4172-80.

Karanian, J.M., Slotnick, S.D., 2014. False memory for context activates the parahippocampal cortex. Cognitive Neuroscience. 5**,** 186-192.

Kim, H., Cabeza, R., 2007. Trusting our memories: Dissociating the neural correlates of confidence in veridical versus illusory memories. Journal of Neuroscience. 27, 12190-12197.

Kim, J., Yassa, M.A., 2013. Assessing recollection and familiarity of similar lures in a behavioral pattern separation task. Hippocampus. 23**,** 287-294.

Kirwan, C. B., & Stark, C. E. L. 2007. Overcoming interference: An fMRI investigation of pattern separation in the medial temporal lobe. Learning & Memory. 14, 625-633.

Klein, C. (2012). Cognitive Ontology and Region- versus Network-Oriented Analyses. Philosophy of Science, 79(5), 952-960. doi: 10.1086/667843

Koutstaal, W., Schacter, D.L., 1997. Gist-based false recognition of pictures in older and younger adults. Journal of Memory and Language. 37**,** 555-583.

Koutstaal, W., Schacter, D.L., Galluccio, L., Stofer, K.A., 1999. Reducing gist-based false recognition in older adults: Encoding and retrieval manipulations. Psychology and Aging. 14**,** 220-237.

Koutstaal, W., 2006. Flexible remembering. Psychonomic Bulletin Review. 13**,** 84-91.

Lacy, J.W., Yassa, M.A., Stark, S.M., Muftuler, L.T., Stark, C.E.L., 2011. Distinct pattern separation related transfer functions in human CA3/dentate and CA1 revealed using high-resolution fMRI and variable mnemonic similarity. Learning & Memory. 18**,** 15-18.

Loftus, E., 2003. Science and society - Our changeable memories: legal and practical implications. Nature Reviews Neuroscience. 4**,** 231-234.

Lyle, K.B., Johnson, M.K., 2006. Importing perceived features into false memories. Memory. 14**,** 197-213.

McCabe, D.P., Geraci, L., 2009. The role of extralist associations in false remembering: A source misattribution account. Memory & Cognition. 37**,** 130-142.

McCarthy, G., Wood, C.C., 1985. Scalp distributions of event-related potentials: An ambiguity associated with analysis of variance models. Electroencephalography and Clinical Neurophysiology. 62**,** 203-208.

McClelland, J.L., McNaughton, B.L., O'Reilly, R.C., 1995. Why there are complementary learning-systems in the hippocampus and neocortex - insights from the successes and failures of connectionist models of learning and memory. Psychological Review. 102, 419-457.

Nessler, D., Mecklinger, A., Penney, T.B., 2001. Event related brain potentials and illusory memories: the effects of differential encoding. Cognitive Brain Research. 10**,** 283-301.

Norman, K.A., 2010. How Hippocampus and Cortex Contribute to Recognition Memory: Revisiting the Complementary Learning Systems Model. Hippocampus. 20**,** 1217-1227.

Odegard, T. N., Koen, J. D., Gama, J. M. 2008. Process demands of rejection mechanisms of recognition memory. Journal of Experimental Psychology: Learning, Memory and Cognition. 34, 1296-1304.

Okado, Y., Stark, C., 2003. Neural processing associated with true and false memory retrieval. Cognitive Affective and Behavioral Neuroscience. 3, 323-34.

Payne, D.G., Elie, C.J., Blackwell, J.M., Neuschatz, J.S., 1996. Memory illusions: Recalling, recognizing, and recollecting events that never occurred. Journal of Memory and Language. 35**,** 261-285.

Pidgeon, L.M., Morcom, A.M., 2014. Age-related increases in false recognition: the role of perceptual and conceptual similarity. Frontiers in Aging Neuroscience. 6**,** 283-283.

Poldrack, R. A. (2006). Can cognitive processes be inferred from neuroimaging data? Trends in Cognitive Sciences, 10(2), 59-63. doi: 10.1016/j.tics.2005.12.004

Roediger, H.L., McDermott, K.B., 1995. Creating false memories - remembering words not presented in lists. Journal of Experimental Psychology-Learning Memory and Cognition. 21**,** 803-814.

Roediger, H.L., Watson, J.M., McDermott, K.B., Gallo, D.A., 2001. Factors that determine false recall: A multiple regression analysis. Psychonomic Bulletin & Review. 8**,** 385-405.

Rugg, M.D., Cox, C.J., Doyle, M.C., Wells, T., 1995. Event-related potentials and the recollection of low and high frequency words. Neuropsychologia. 33**,** 471-84.

Rugg, M.D., Mark, R.E., Walla, P., Schloerscheidt, A.M., Birch, C.S., Allan, K., 1998. Dissociation of the neural correlates of implicit and explicit memory. Nature. 392**,** 595-598.

Rugg, M.D., Curran, T., 2007. Event-related potentials and recognition memory. Trends in Cognitive Sciences. 11**,** 251-7.

Schacter, D.L., Norman, K.A., Koutstaal, W., 1998. The cognitive neuroscience of constructive memory. Annual Review of Psychology. 49**,** 289-318.

Schacter, D.L., Slotnick, S.D., 2004. The cognitive neuroscience of memory distortion. Neuron. 44**,** 149-160.

Schmid, J., Herholz, S.C., Brandt, M., Buchner, A. 2010. Recall-to-reject: the effect of category cues on false recognition. Memory. 18, 863-882.

Senkfor, A.J., Van Petten, C., 1998. Who said what? An event-related potential investigation of source and item memory. Journal of Experimental Psychology-Learning Memory and Cognition. 24**,** 1005-1025.

Stark, S.M., Yassa, M.A., Lacy, J.W., Stark, C.E.L., 2013. A task to assess behavioral pattern separation (BPS) in humans: Data from healthy aging and mild cognitive impairment. Neuropsychologia. 51**,** 2442-2449.

Thomas, A.K., Loftus, E.F., 2002. Creating bizarre false memories through imagination. Memory & Cognition. 30**,** 423-431.

Treves, A., Rolls, E.T., 1994. Computational analysis of the role of the hippocampus in memory. Hippocampus. 4, 374-91.

Vilberg, K.L., Moosavi, R.F., Rugg, M.D., 2006. The relationship between electrophysiological correlates of recollection and amount of information retrieved. Brain Research. 1122**,** 161-70.

Vilberg, K. L., & Rugg, M. D. (2009). Functional Significance of Retrieval-Related Activity in Lateral Parietal Cortex: Evidence From fMRI and ERPs. Human Brain Mapping, 30(5). doi: 10.1002/hbm.20618

Voss, J.L., Federmeier, K.D., 2011. FN400 potentials are functionally identical to N400 potentials and reflect semantic processing during recognition testing. Psychophysiology. 48**,** 532-546.

Wiese, H., Daum, I., 2006. Frontal positivity discriminates true from false recognition. Brain Research. 1075**,** 183-192.

Wilding, E.L., Rugg, M.D., 1996. An event-related potential study of recognition memory with and without retrieval of source. Brain. 119**,** 889-905.

Wilding, E. L. 2000. In what way does the parietal ERP old/new effect index recollection? International Journal of Psychophysiology, 35(1), 81-87.

Wolk, D.A., Schacter, D.L., Lygizos, M., Sen, N.M., Holcomb, P.J., Daffner, K.R., Budson, A.E., 2006. ERP correlates of recognition memory: effects of retention interval and false alarms. Brain Research. 1096**,** 148-62.

Woodruff, C.C., Hayama, H.R., Rugg, M.D., 2006. Electrophysiological dissociation of the neural correlates of recollection and familiarity. Brain Research. 1100**,** 125-135.

Yassa, M.A., Lacy, J.W., Stark, S.M., Albert, M.S., Gallagher, M., Stark, C.E.L., 2011. Pattern Separation Deficits Associated With Increased Hippocampal CA3 and Dentate Gyrus Activity in Nondemented Older Adults. Hippocampus. 21.

Yassa, M.A., Stark, C.E.L., 2011. Pattern separation in the hippocampus. Trends in Neurosciences. 34.

Yonelinas, A.P., 2002. The Nature of Recollection and Familiarity: A Review of 30 Years of Research. Journal of Memory and Language. 46**,** 441-517.